

Distribution, Abundance, Feeding Growth and Mortality of Fish Larvae Associated with the Mississippi River Discharge Plume, and the Potential Impacts of Hypoxia

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Abstract

From 1986–1992 we made cruises during all seasons to the Mississippi River discharge plume to collect ichthyoplankton using a neuston net (1 x 2 m; .947 mm) and tucker trawl (1 x 1 m; 0.335 mm); CTD casts were made to collect environmental data. Sampling stations were positioned using AVHRR satellite imagery (visible channel) along 15–25 km transects that radiated from the delta outward.

The hydrography in the vicinity of the plume consists of three distinct water masses, a shallow lens of low salinity plume water, high salinity Gulf of Mexico shelf water and the 6–8km wide frontal or mixing zone between plume and shelf waters.

Fish larvae are abundant in the vicinity of the discharge plume in general, but are especially concentrated in the frontal region, e.g., average neuston catches were 6-fold higher than at plume stations and 12-fold higher than at shelf water stations.

The described hydrography promotes strong hydrodynamic convergence within the frontal zone. We used surface drifters to measure apparent surface convergence rates at turbidity fronts of up to 0.8 m/sec. We used an advection diffusion model to simulate larval densities in surface waters at the frontal convergence zone

that approximated the mean and median observed densities within the frontal zone.

We deployed radio tracked surface drifters and repeatedly sampled nearby over time to determine if larvae could be retained in the vicinity of the plume, or were advected westward by the average surface flow off the Mississippi Delta. A clockwise circulation with a radius of curvature of about 50km was identified and acted to retain larvae in the vicinity of the plume.

The diet of striped anchovy, *Anchoa hepsetus*, larvae was investigated to determine if fish larvae in the frontal zone were deriving a trophic advantage from the potential food resources concentrated there. The diet consisted of a wide array of prey items including various microcrustaceans (e.g., amphipods, cladocerans, copepods and ostracods) diatoms, larvaceans and polychaete larvae, but according to both frequency of occurrence and number of prey items, copepods and diatoms were the dominant foods consumed. Diatoms occurred more frequently and more numerous at plume and shelf stations (43 percent and 39 percent and 72 percent and 75 percent, respectively), but copepods were the most frequently occurring (49 percent) and most numerous (48 percent) prey items at frontal stations. Because copepods are larger and have a slightly higher C:N ratio striped anchovy larvae in frontal waters may consume a more nutritious diet.

Otolith microstructure techniques were used to determine age and estimate growth rates to determine if larvae in the vicinity of the plume in general, or the frontal waters in particular, grow faster. King mackerel, *Scomberomoras cavalla*, larvae from the Mississippi plume region grew significantly faster than larvae from other areas (0.95 vs. 0.79 mm/d), while Spanish mackerel, *S. maculatus*, and little tunny, *Euthynnus alletteratus*, from the plume did not. Spanish mackerel, yellowfin tuna, *Thunnus ablacares*, and striped anchovy larvae in the vicinity of the discharge plume grew faster at intermediate salinities, i.e., the frontal zone (1.0 vs. 1.3, 0.75 vs. 0.6 and 1.05 vs. 0.85 mm/d, respectively). We regressed \log_e of SL on age for the descending limb of plots for these same species to estimate daily instantaneous mortality rates. Mortality rates were higher in the vicinity of the plume for Spanish mackerel, little tunny, and striped anchovy (0.6 vs. 0.3, 0.9 vs. 0.7 and 0.23 vs. 0.12, respectively).

A relative survival model

$$N_t = N_0 e^{-zt}$$

where

z = daily instantaneous mortality rate

t = L_{\max} /growth rate (mm)

L_{\max} = a 25-mm size refuge

was used to evaluate the advantage of faster growth vs. the disadvantage of increased mortality for Spanish mackerel larvae. Survival was much more sensitive to changes in mortality than growth, suggesting that the specific demographics prevalent in the plume environment may not favor survival and recruitment in the Mississippi River discharge plume.

Introduction

There is considerable circumstantial evidence worldwide that river plumes influence the mechanisms underlying fish production (i.e., growth, mortality and recruitment), recruitment being the most important since it is the largest contributor to variation in fish production. Major fisheries have been eliminated or have declined when river flows were controlled. For example, filling of the Aswan Dam began on the Nile River in 1965 and was completed in 1969, during which time the flow was decreased by $40 \text{ km}^3 \text{ yr}^{-1}$, with a concomitant decline in primary production off the delta. Egyptian fishery catches in the Mediterranean Sea declined from 37,800t in 1962 to 7,142t in 1976, with an attendant decline in community structure (Bebars and Lasserre, 1983). The largest river in North America, the Mississippi, is no exception. A major feature influencing the ocean environment of the Gulf of Mexico—it annually discharges an average $1.83 \times 10^4 \text{ m}^3 \text{ S}^{-1}$ (Gunter, 1979) of freshwater, nutrients, and suspended materials. Fishery landings from the fertile fishery crescent surrounding the Mississippi River delta are extraordinary, accounting for approximately 80 percent of the total commercial landings from the Gulf of Mexico (NMFS, 1994).

There is concern about how the periodic occurrence of a major hypoxia zone off the Mississippi River may influence the valuable fisheries associated with the river. The purpose of this brief report is to summarize the results of research on the recruitment dynamics, i.e., abundance, feeding, growth, and mortality, of fish larvae associated with the Mississippi River discharge plume, and discuss the possible significance of these results to hypoxia and its potential impact on fish production.

Results And Discussion

From 1986–1993 we conducted research cruises during both low (summer-fall) and high (spring) flow regimes to the Mississippi River discharge plume. Plankton samples were collected at stations 4–6 km apart along 15–25 km transects that radiated out from the delta, and were positioned using AVHRR satellite imagery (visible channel) to cross from the plume into Gulf of Mexico shelf waters. Plankton was collected with neuston net (1 x 2 m; 0.947 mm) and Tucker trawl (1 x 1 m; 0.335 mm); CTD casts were made to obtain environmental data at each station.

The water column in the vicinity of the discharge plume has a characteristic hydrographic structure created by the abutment of water masses with distinctly different densities (Grimes and Finucane, 1991; Govoni and Grimes, 1992). Lighter plume waters are represented by a shallow lens of low salinity water overlying heavier high salinity Gulf of Mexico shelf waters; the 6–8 km wide frontal, or mixing, zone between these two water masses is where isohalines are closely spaced and approach the surface (Figure 48). Turbidity fronts, represented by sharp color discontinuities, are the seaward projection of concentrated suspended particulate matter, and they are often nested within the frontal zone (Garvine and Monk, 1974).

Phytoplankton, zooplankton and fish larvae are concentrated in the vicinity of the plume in general and the frontal region in particular. For example, average surface phytoplankton biomass, macrozooplankton displacement volume and neustonic ichthyoplankton catch rates were about 4, 2 and 6 fold greater in frontal waters than in adjacent plume and shelf waters (Grimes and Finucane, 1991; see also Govoni *et al.*, 1989 and Govoni and Grimes, 1992).

Surface waters converge at plume fronts, pri-

marily due to strong horizontal density gradients and resulting pressure gradients that are produced within and below the frontal layer. Cross frontal circulation is characterized by vigorous convergence on both sides of the front, typically higher on the high density (seawater) side than on the low density (plume) side, e.g., average 0.2 and 0.1 m sec⁻¹ for the Mississippi River plume (Govoni and Grimes, 1992). As surface waters converge, planktonic organisms move passively with the water toward the front where converging water masses move downward with gravity. Surface seeking and buoyant organisms accumulate at the surface as they resist downward movement. This is local, but important, transport mechanism that can concentrate larval fish and zooplankton and account for the high densities of these properties observed at fronts. Govoni and Grimes (1992) measured surface convergence velocity in the Mississippi River up to 0.8 m sec⁻¹. Observed velocity was always greater than the velocity calculated from the density alone (Figure 49) because the observed velocity is the sum of the density driven velocity plus the tidally driven velocity inherent in shelf waters. They used the advection diffusion model of (Olson and Backus (1985) to simulate surface densities of fish larvae at the front that agreed well with observed values (Figure 50).

Having observed the distribution and abundance of these properties, as well as the hydrographic structure and hydrodynamics Grimes and Finucane (1991) developed a modification of the short food chain hypothesis explaining how the Mississippi River might act to enhance recruitment of associated fish larvae. This hypothesis states that fish larvae concentrated in the vicinity of the plume in general, and the frontal region in particular, would take advantage of abundant food resources and consume a superior diet, grow faster and thus experience a shorter larval stage duration and survive better. Implicit in this hypothesis is that fish larvae in the vicinity of the discharge plume are not advected away from

the rich plume environment by the low average westward flowing surface currents that prevail off the Mississippi River delta during the period of interest (summer-fall) (Wiseman and Dinnel, 1988).

Radio tracked surface drifters were deployed and repeatedly sampled nearby over time to determine if fish larvae were retained in the vicinity of the plume or were advected away (Grimes and Wiseman unpublished). The surface drifters were entrained in a tongue of Gulf of Mexico shelf water that intruded into the Louisiana Bight and rotated clockwise with a radius of curvature of about 50km (Figure 51). The average variation in abundance of fish larvae in surface collections suggested that the same assemblage of fish larvae was repeatedly sampled nearby the surface drifters because the coefficient of variation in total abundance along drifter tracks was two to four fold less than the variation among samples collected along transects that intentionally crossed plume, front and shelf waters (Table 3). These results suggest that, at least in this instance, a clockwise circulation existed in the vicinity of the plume that acted to retain fish larvae.

Research findings thus far are not totally in accord with the first element of the short food chain hypothesis, i.e., it cannot be stated unequivocally that fish larvae associated with the Mississippi River plume are conferred a trophic advantage. Spot, *Leiostomus xanthurus*, larvae collected off the Mississippi River plume ate twice as many food organisms as did larvae in Gulf of Mexico shelf waters (Govoni and Chester, 1990). However, organisms within the plume were mostly small (tintinnids, copepod nauplii, pelecypod veligers and invertebrate eggs), whereas organisms eaten in shelf waters were larger (copepodites and adult copepods). Because the volume and nutritional quality of gut contents of larvae from the two areas were roughly equivalent, they concluded that larvae in the plume gained no trophic advantage. Similarly,

Powell *et al.* (1990) used morphological, gut content and recent growth criteria to evaluate nutritional condition of spot larvae associated with the Mississippi discharge, and could not consistently demonstrate an advantage. A diet study on striped anchovy, *Anchoa hepsetus*, collected along transects crossing plume, front and shelf waters showed that diatoms and copepods were by far the dominant food items, and that the larger more nutritious copepods occurred more frequently and accounted for the highest percentage of food items in guts of larvae collected in frontal waters, followed by plume waters then shelf waters (McNeil and Grimes, 1995). A suite of biochemical indices to nutritional condition (RNA/DNA ratio, percent protein and CS and LDH enzyme systems), were examined on striped anchovy collected along the same transects off the Mississippi plume; larvae collected in frontal waters were in the highest nutritional conditions (Torres *et al.* unpublished). Furthermore, in a recent review of the influence of riverine plumes worldwide on fish larvae Grimes and Kingsford (in press) found that certain taxa, e.g., small opportunistic species, appear to be associated with plumes and may be better adapted than larger more competent larvae of other species to take advantage of abundant food resources around plumes and their fronts.

The second element of the hypothesis states that fish larvae that are conferred a trophic advantage will respond by growing faster, and there is some evidence that growth of some fish larvae, as determined from otolith microstructure, may be enhanced. Growth of king mackerel, *Scomberomorus cavalla*, was higher off the Mississippi River plume (0.95 mm d^{-1}) than at other locations in the Gulf of Mexico (0.79 mm d^{-1}) (DeVries *et al.*, 1990). However, superior growth off the plume was not demonstrated for Spanish mackerel, *S. maculatus*, (DeVries *et al.*, 1990), or little tunny, *Euthynnus alletteratus*, (Allman and Grimes unpublished). Other results on Spanish mackerel, (Grimes and De Vries unpublished,

Figure 52) as well as those on yellowfin tuna, *Thynnus albacares*, (Lang *et al.*, 1994) and striped anchovy, *Anchoa hepsetus*, (Day, 1993), suggest that larvae associated with the Mississippi plume grow faster at intermediate salinities, i.e., frontal waters (0.6 vs. 0.75 mm d⁻¹, respectively for yellowfin tuna and striped anchovy).

The final element of the hypothesis states that faster growth leads to shorter duration of the larval stage and better survival, with the caveat that the same dynamics that concentrate prey of fish larvae might also concentrate their predators. There is little evidence to evaluate this element of the hypothesis. Grimes and DeVries (unpublished) estimated instantaneous rates of natural mortality for Spanish mackerel and king mackerel using a catch-curve approach (i.e., regressing the log of frequency on age of the descending limb of age-frequency histograms). Instantaneous natural mortality estimates were approximately 0.3d⁻¹ away from the plume and 0.6d⁻¹ or higher in the vicinity of the plume. For little tunny, instantaneous natural mortality was slightly higher in the vicinity of the Mississippi River plume (0.94d⁻¹) than in the Gulf of Mexico off Panama City, Florida (0.85d⁻¹) (Allman and Grimes unpublished). Similar analyses for striped anchovy in water masses off the Mississippi River suggest that natural mortality in the front (0.13d⁻¹) and plume (0.23d⁻¹) may be higher than that experienced in shelf waters (0.09d⁻¹) (Day, 1993). Conversely, yellowfin tuna (Lang *et al.*, 1994) experience higher natural mortality at fronts (0.41d⁻¹) than in the plume area in general (0.16d⁻¹). These differences in mortality rates should be interpreted with caution. Application of catch curve or survivorship analysis to estimate instantaneous mortality rates assumes equal vulnerability to capture by the sampling gear for all ages used in the analysis. Faster growth rates might lead to biased mortality estimates because fast growing larger larvae become less vulnerable to capture and may be under represented at the older ages used in the analysis. Although these

results are tentative they do not support the contention that higher growth rates of larvae associated with river plumes lead to better survival.

To summarize the results of evaluating the elements of the short food chain hypothesis with respect to the Mississippi River, it appears that some species of fish larvae, opportunistic ones, are able to take advantage of abundant prey resources. Also, some species of fish larvae appear to grow faster, but mortality rates may also be higher. So, whether this hypothesis is valid and the population dynamics of fish larvae in the vicinity of river plumes favor recruitment, depends upon the relative magnitude of growth and mortality. A simple and convenient way of evaluating the relative importance of growth and mortality is to use the expression of exponential decay in population size with time

$$N_t = N_0 e^{zt}$$

where

N_t = population at time t

N_0 = initial population

z = instantaneous mortality.

Z can be directly estimated, while $t = L_c/g$ (where L_c = a critical size refuge where mortality decreases markedly) and g = growth rate that is also directly estimated. The product of zt is an exponent that determines the decrease in N_0 . Obviously, the effect of z on N_0 (survival to the critical size, L_c) is much greater than g , because z is a direct multiplier and g is a fractional multiplier (the divisor of L_c). Thus, incremental changes in mortality will have a much larger effect on survival and recruitment than incremental changes in growth rate. So, if physical and biological conditions in the vicinity of the Mississippi River plumes aggregate larval fish prey that results in a trophic advantage and faster growth, but also aggregates predators and

increases the mortality rate on larvae, the disadvantage of increased mortality may well outweigh the advantage of faster growth, and increased survival and recruitment will not be the result. However, I emphasize that accurate larval mortality rate estimates are difficult to obtain using the time specific approach usually taken, due mainly to sampling bias associated with gear selectivity and the contagious distribution of fish larvae in time and space.

In summarizing their review of the effects of riverine plumes on fish larvae and their recruitment dynamics, Grimes and Kingsford (in press) offer two alternatives to the short food chain hypotheses. One alternative possibly explaining the apparent favorable effect of river plumes on recruitment, the total larval production hypothesis, is that trophic conditions support such high total production of fish larvae that negative effects of unfavorable dynamics are overridden. That is, high primary and secondary production associated with plumes may simply support such high total production of fish larvae that the specific population dynamics at plumes are not often relevant. A second alternative is that plumes and associated circulations facilitate the retention of larvae within an area. The presence of food would of course be important, but variation in physical retention rather than production may explain variation in recruitment; as argued for the member/vagrant hypothesis of Sinclair (1988).

The relationship between hypoxia and the recruitment dynamics of fish larvae in the vicinity of the Mississippi River discharge is in fact unknown, but there are several potentially important possibilities that can be discussed. The present understanding is that the hypoxia is due to both the effects of stratification of fresh and marine waters that restricts vertical reoxygenation of bottom waters, and the oxygen consuming breakdown of organic material mostly derived from high plankton production driven by river

borne nutrients. While the hypoxia problem is believed to have been exacerbated by nutrient enrichment of the Mississippi River, the high nutrient load of the river and resulting high productivity associated with the discharge area is also vital to maintaining valuable Gulf of Mexico fisheries (e.g., approximately 80 percent of commercial fishery landings are taken from the region of riverine influence).

Hypoxia and the larvae of valuable fishery species may sometimes co-occur in time and space, almost certainly leading to larval mortality when this occurs. The hypoxic zone is generally located from off the Mississippi River delta westward along the Louisiana coast, and although it can occur in the winter and fall it most consistently occurs from mid-May to mid-September. A number of valuable species spawn at this time in the gulf, and their larvae are abundant off the Mississippi River delta, e.g., both king mackerel (Grimes *et al.*, 1990) and Spanish mackerel (Grimes and DeVries unpublished), cobia (Ditty and Shaw, 1992), dolphin (Ditty *et al.*, 1994) and yellowfin tuna (Lang *et al.*, 1994). Several valuable reef fishes, e.g., gray snapper, vermilion snapper and red snapper also spawn at that time, and while their larvae are collected off the delta (Grimes *et al.* unpublished, Lyczkowski-Shultz unpublished, Comyns unpublished) the adults spawn over hard bottom and thus spawning is probably not associated with the river discharge. Fish larvae are most abundant in near surface waters off the Mississippi plume (Govoni *et al.*, 1989), and the hypoxia is typically associated with bottom waters but it can extend up into the water column. Thus, differing vertical distributions of the hypoxic water and fish larvae may ameliorate potential negative impacts of hypoxia on larvae. However, the concentration of larvae in the frontal region may extend deeper into the water column because the hydrodynamic convergence that acts to concentrate larvae (Govoni and Grimes, 1992) continues unabated to the bottom on the high density (seawater) side of the

convergence zone (Govine and Monk, 1974).

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Table 3.

Comparisons of the average variation (Coefficient of variation, CV) in total ichthyoplankton catch at stations along drifter tracks to CV's for catches made at stations along transects that intentionally sampled plume, front and shelf waters.

	CV
Along drifter tracks	
• Gimes and Wiseman (unpublished)	61 (fall)
Among plume, front and shelf waters	
• Grimes and Finucane (1991)	235 (fall)
• Govoni and Grimes (1992)	140 (fall) 129 (spring)

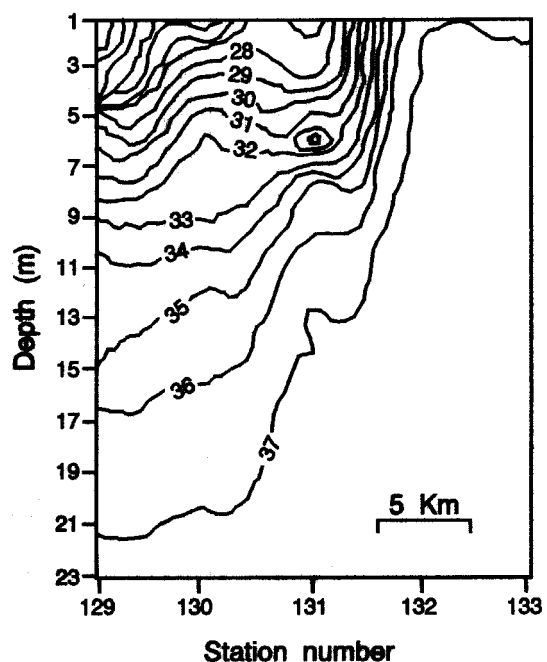


Figure 48.

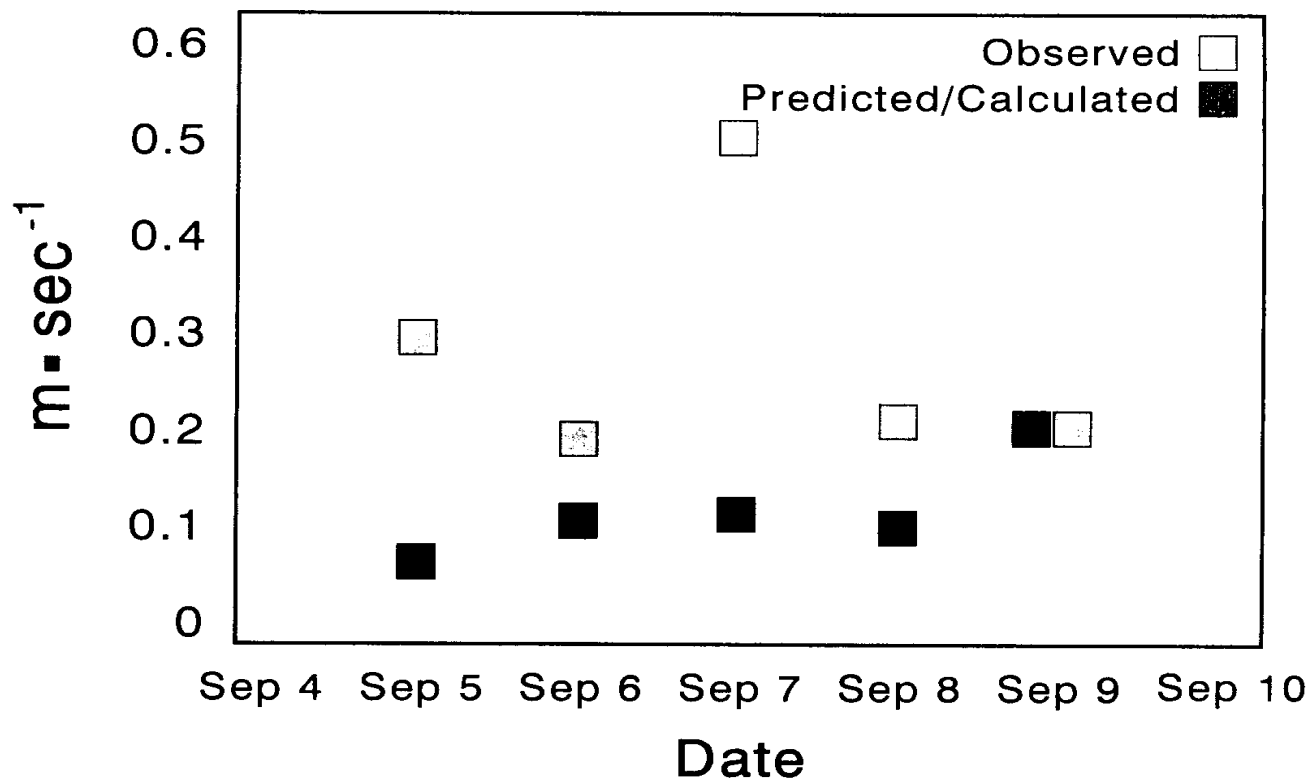


Figure 49.

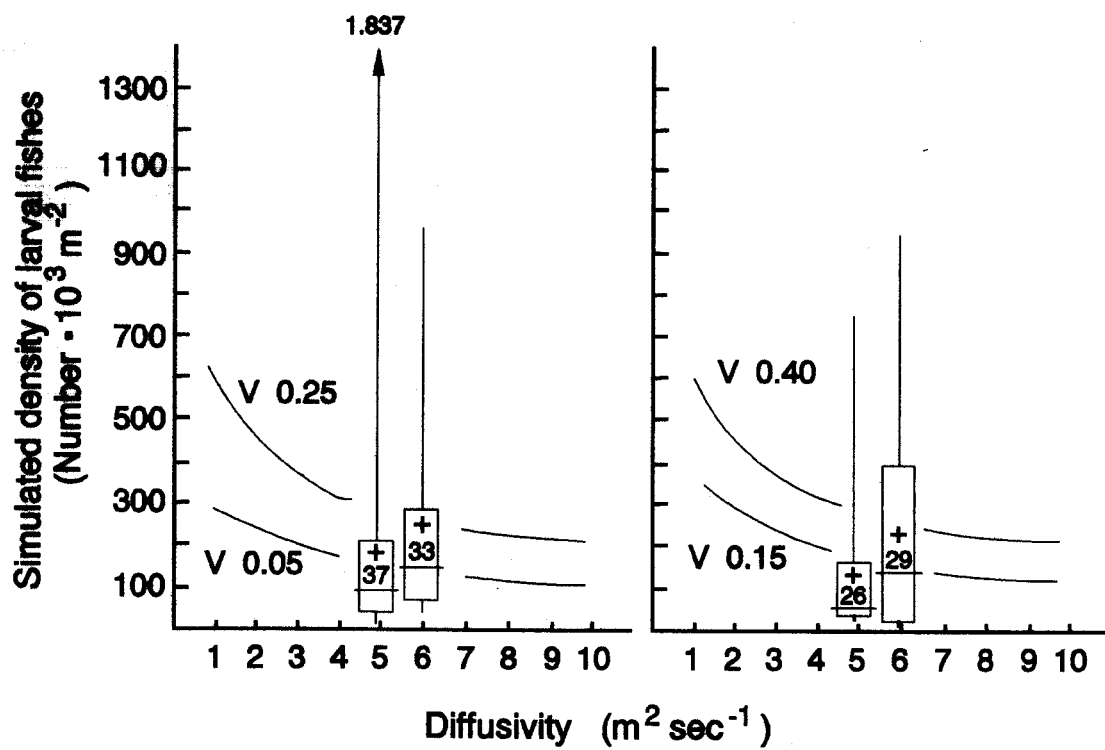


Figure 50.

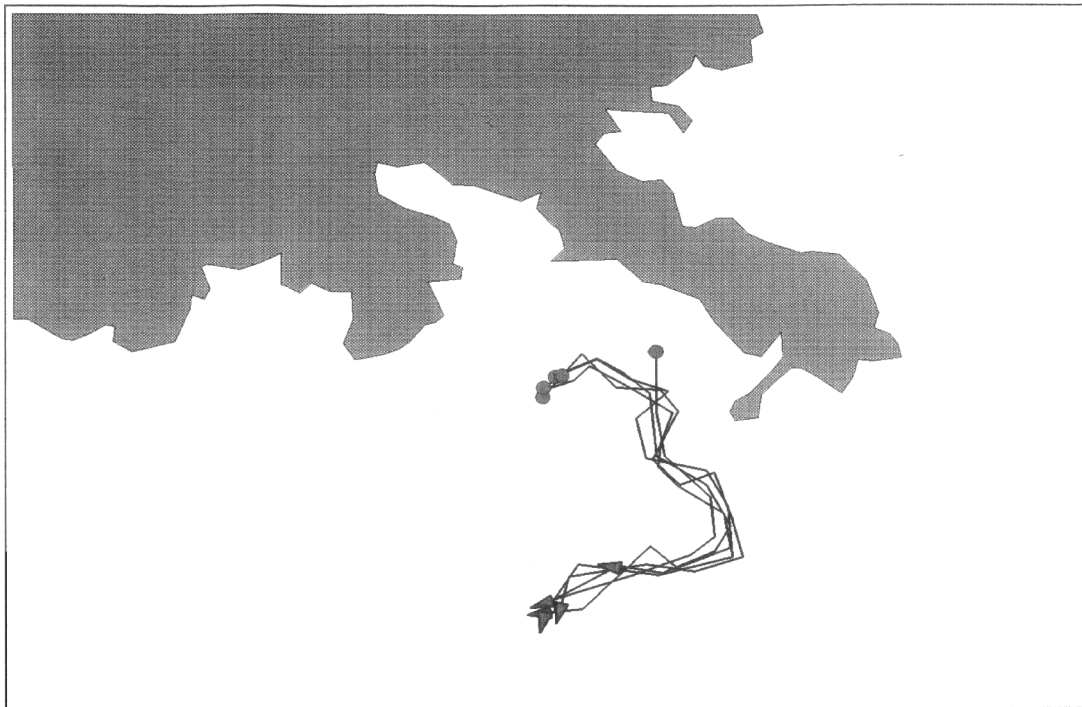


Figure 51.

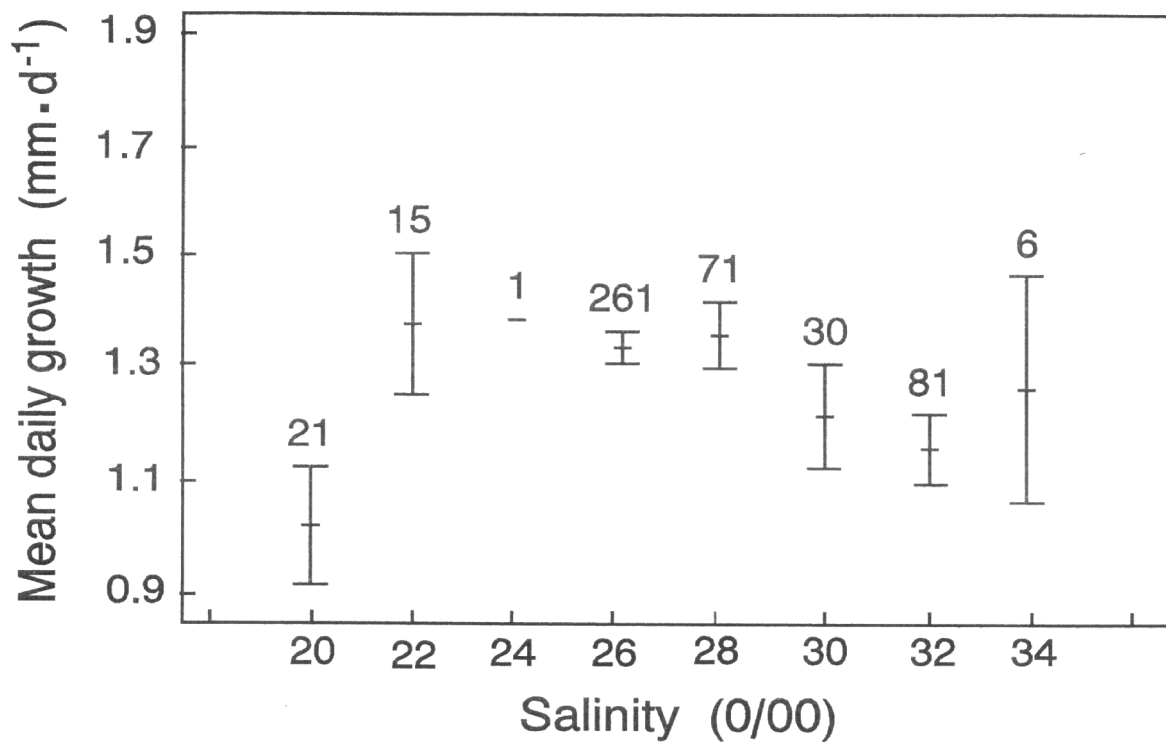


Figure 52.

Presentation Discussion

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Fred Bryan (*National Biological Service—Baton Rouge, LA*) commented that between 11-19 days of age, fish may be approaching the size where they are no longer equally disposed to the gear being used. Therefore, the estimate of mortality could be indicative of the organisms having become more nektonic than planktonic and thus are no longer available to a neuston or Tucker trawl.

Churchill Grimes agreed with Fred Bryan's observation. He said that estimating larval mortality is an extremely difficult task. He attempted to estimate larval mortality by following the same patch of larvae through a specified period of time. However, because the variation in catch was so great, it was impossible to complete the study.